

## Biological relevance of polyploidy: ecology to genomics

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# Origins, establishment and evolution of new polyploid species: *Senecio cambrensis* and *S. eboracensis* in the British Isles

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Two new polyploid species of *Senecio* have originated in the British Isles in recent times following hybridization between native *S. vulgaris* ( $2n = 40$ ) and introduced *S. squalidus* ( $2n = 20$ ). One of these is the allohexaploid *S. cambrensis* ( $2n = 60$ ), the other is the recombinant tetraploid *S. eboracensis* ( $2n = 40$ ). We review what is known about when and how each species originated, and their reproductive isolation from parents due to high selfing rates. We also review evidence that suggests *S. cambrensis* may have undergone rapid genome evolution since its origin, and comment on the risks of extinction to each species due to chance factors operating during the early establishment phase. The discovery of both species soon after their origin provides an unparalleled opportunity to examine two different but related forms of speciation following hybridization between the same parent species. Further detailed study of the ecology and genomics of *S. cambrensis* and *S. eboracensis* will help improve our understanding of the process of polyploid speciation in plants. © 2004 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2004, **82**, 467–474.

**ADDITIONAL KEYWORDS:** allopolyploidy – genome evolution – hybridization – minority type disadvantage – reproductive isolation – selfing – speciation.

## INTRODUCTION

The discovery of a new polyploid species in the wild soon after its origin presents the opportunity to examine numerous phenomena concerning polyploid speciation and evolution. Because many polyploid species originate on more than one occasion and at different locations (Soltis & Soltis, 1993), the study of polyploid speciation can be replicated in the wild. Moreover, it is often feasible to resynthesize artificially new polyploids from their known parents (Levin, 2002) and subject synthetic material to detailed comparative analysis (Ingram & Noltie, 1989). Although it appears obvious that newly originated polyploid species pro-

vide an excellent resource for studying the process of polyploid speciation in detail, such species have until now been underused for this purpose.

Five angiosperm species are known to have originated via allopolyploidy in recent times, i.e. within approximately the past 150 years. These are *Spartina anglica* C.E. Hubbard, which originated in Southampton Water, UK, in the 1880s (Raybould *et al.*, 1991; Ainouche, Baumel & Salmon, 2004 – this issue), *Tragopogon mirus* Ownbey and *T. miscellus* Ownbey, both of which originated in Washington State, USA, in the mid-1900s (Ownbey, 1950; Roose & Gottlieb, 1976; Soltis & Soltis, 1989; Soltis *et al.*, 2004 – this issue), *Senecio cambrensis* Rosser, which originated in North Wales, UK, also in the mid-1900s (Rosser, 1955; Ashton & Abbott, 1992a; Ingram & Noltie, 1995; Abbott & Lowe, 1996), and *Cardamine schulzii* Urbanska, which originated in Switzerland in the latter part of the 20th century (Urbanska *et al.*, 1997). Another

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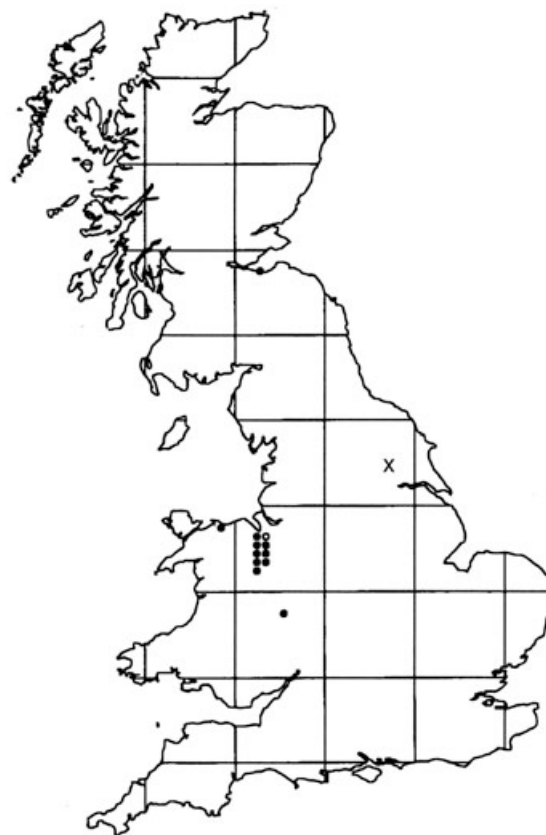
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polyploid species, *Senecio eboracensis* Abbott & Lowe, also known to have originated very recently (Lowe & Abbott, 2003), appears to have formed through recombinant polyploid speciation. In this case a substantial portion of the genome of the diploid parent may have replaced part of a genome of the tetraploid parent following interspecific hybridization (Abbott *et al.*, 2003).

Molecular evidence has been used to resolve the identities of the parents of each of these six new species and to determine whether they originated on more than one occasion. However, only recently have detailed studies been carried out or initiated on them to investigate other aspects of the speciation process, namely establishment and the possibility of rapid structural and functional genomic change following their origin (see Levin, 2002). Here we focus on the two new *Senecio* species that have originated in the UK during the past 60 years or so. We review work that has examined their origins and establishment in the wild, giving particular attention to how they are reproductively isolated from their parent taxa, and counter the minority type disadvantage (Levin, 1975, 2002; Felber, 1991; Husband, 2000; see also Husband, 2004; Pannell, Obbard & Buggs, 2004 – both this issue), which many new polyploid species face when occurring at low frequency in sympatry with a parent directly after their origin. In addition, we review work on *S. cambrensis*, which suggests that this species is capable of rapid genomic evolution following its origin. We also comment on the risk of extinction due to chance that a new species faces during the early establishment phase.

#### ORIGINS OF *S. CAMBRENSIS* AND *S. EBORACENSIS*

*Senecio cambrensis* was first recorded by H. E. Green in 1948 near Cefn-y-bedd, Clwyd, North Wales (Rosser, 1955). It was later described as a new species by Rosser (1955) from material collected from a roadside near Ffrith, not far from Cefn-y-bedd. The species has a chromosome number of  $2n = 60$ , and a plant very similar morphologically to wild material was produced by S. C. Harland and A. Haygarth Jackson by colchicine treatment of the synthetic hybrid *S. squalidus*  $\times$  *vulgaris* ( $2n = 30$ ). It was concluded that the new species was an allohexaploid, which originated by hybridization between native *S. vulgaris* ( $2n = 40$ ) and introduced *S. squalidus* ( $2n = 20$ ) followed by chromosome doubling. Because *S. squalidus* was not present in the wild in the British Isles until 1792 (Abbott, 1992; Harris, 2002), and was not recorded in North Wales until approximately 1910 (Kent, 1963), *S. cambrensis* is likely to have originated in the UK only shortly before it was first recorded. The new species is now firmly established in North Wales



**Figure 1.** The distribution of *S. cambrensis* (dots) and *S. eboracensis* (x) in Britain. For *S. cambrensis*, each dot represents at least one record in a 10-km square of the National Grid: (○) pre 1950, (●) 1950 onwards, mapped by the Biological Records Centre, Centre for Ecology and Hydrology.

in the area around Wrexham and the villages nearby (Fig. 1). It has also been recorded at Mochdre, near Colwyn Bay, approximately 55 km away, and at Ludlow, Shropshire, England (Ingram & Noltie, 1995).

In 1982, *S. cambrensis* was found on several waste-sites in Edinburgh, Scotland (Abbott, Ingram & Noltie, 1983). An herbarium specimen at the Royal Botanic Garden, Edinburgh, showed that the species had been collected previously from Edinburgh in 1974, but was misidentified as *S. vulgaris*  $\times$  *S. squalidus*. A survey of isozyme variation in the species and its parents in both North Wales and in Edinburgh revealed that it had originated independently at both locations (Ashton & Abbott, 1992a). Moreover, the results indicated that the new species could have originated on three different occasions in North Wales, twice in the Wrexham area and once at Mochdre. However, the possibility that the pattern of isozyme variation in Welsh *S. cambrensis* was caused by segregation following homoeologous chromosome pairing and recombination

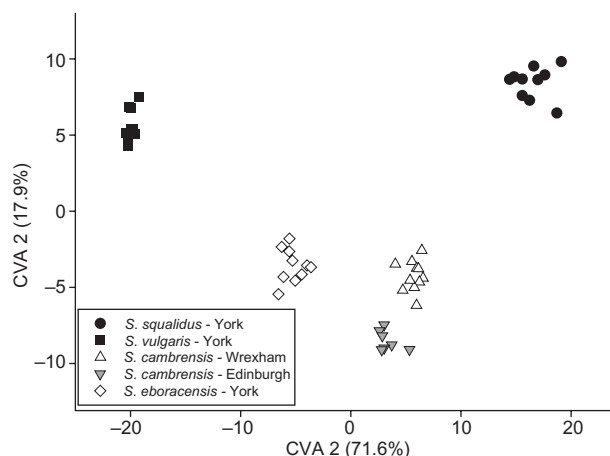
after a single origin, rather than by multiple origins, could not be ruled out (Ashton & Abbott, 1992a).

Additional evidence of separate origins of *S. cambrensis* in North Wales and Edinburgh was obtained by Harris & Ingram (1992), who showed that the chloroplast genome of Welsh material contained an insertion of ~330 bp that was absent from the cpDNA of Edinburgh plants. Further analysis of cpDNA RFLP variation in *S. cambrensis* and its two parents produced strong evidence that *S. vulgaris*, which was found to be polymorphic for the presence/absence of the cpDNA insertion, served as the maternal parent of both Welsh and Edinburgh *S. cambrensis* (Lowe & Abbott, 1996). This agrees with the finding that crosses between the two parents are normally only successful when *S. vulgaris* is used as the maternal parent (Ingram, Weir & Abbott, 1980; Lowe & Abbott, 2000; but see Ingram, 1977, for rare exceptions).

A morphometric comparison of *S. cambrensis* with its parents *S. vulgaris* and *S. squalidus* raised in a common environment showed that *S. cambrensis* is phenotypically largely a composite of traits possessed by one or the other parent (Lowe & Abbott, 1996). However, for five characters – capitulum length, capitulum bract length, longest leaf length, seed length and number of pores per pollen grain – its mean was significantly greater than those of either parent. Edinburgh and Welsh (Wrexham) *S. cambrensis* differ significantly for several traits and are placed into separate groups by a canonical variate analysis (Fig. 2). However, these two groups occur close to each other and distant from the parent taxa. It can be concluded therefore that the two forms of *S. cambrensis* differ for several traits, but in general are phenotypically very similar to each other.

A final point of interest concerning the origin of *S. cambrensis* is its relationship to another allohexaploid species, *S. teneriffae* Schultz Bip., which is endemic to the Canary Islands. These two species are interfertile and morphologically very similar. Preliminary results of allozyme and nuclear rDNA RFLP analyses indicate that *S. teneriffae* arose from a cross between *S. vulgaris* and *S. glaucus*, rather than between *S. vulgaris* and *S. squalidus* (Lowe & Abbott, 1996). However, a more detailed investigation is required to confirm this.

*Senecio eboracensis* was first recorded by R. J. Abbott and D. F. Marshall on wasteground in York, England, in 1979 (Fig. 1), and was later demonstrated to be tetraploid ( $2n = 40$ ) and highly fertile. It was initially regarded as a radiate form of *S. vulgaris* and given the name York radiate groundsel (Irwin & Abbott, 1992). Only recently has it been formally described as a new species (Lowe & Abbott, 2003). Because *S. squalidus*



**Figure 2.** Canonical variate plot for *S. cambrensis* (Edinburgh and Welsh, i.e. Wrexham, lineages), *S. eboracensis*, and their parent taxa, *S. vulgaris* and *S. squalidus*. Each point represents the canonical variate scores (CVA1 vs. CVA2) for an individual within a taxon/lineage. The CVA was conducted on a suite of 22 morphological traits measured on plants grown in a common environment. The percentages of total variance accounted for by CVA1 and CVA2, respectively, are indicated in parentheses. Details of traits measured and experimental growth conditions are available from A.J.L. upon request.

did not become established in York and the surrounding area until the early 1960s it is thought unlikely that *S. eboracensis* originated much before the time it was discovered (Lowe & Abbott, 2003). Its status as a derivative of *S. vulgaris* × *S. squalidus* was established from isozyme evidence (Irwin & Abbott, 1992), in that it possesses an additive esterase phenotype that combines the distinctive  $\alpha$ Est-1 and  $\beta$ Est-1 phenotypes expressed by *S. vulgaris* and *S. squalidus*, respectively. It also exhibits an intermediate morphology when grown in a common environment, combining characters present in one or other of its parents, as well as exhibiting some intermediate and also several novel traits (Irwin & Abbott, 1992). Canonical variate analysis conducted on material raised in a common environment with parent taxa and *S. cambrensis* (see above) placed *S. eboracensis* as intermediate to the parents and close but separate from *S. cambrensis* (Fig. 2). Most notably, it produces achenes (2.5–3.5 mm in length) that are longer than those of either parent (<2.5 mm), has longer and more dissected leaves, and produces large, four-pored pollen, in contrast to the three-pored pollen of its parents. In these and other traits it is very similar to *S. cambrensis*, but can be distinguished from the hexaploid by several morphological characters including capitulum width, number of ray florets, number and length of involucre



bracts and leaf shape, and also by the fact that it is tetraploid (Lowe & Abbott, 2003).

A preliminary analysis of the genomic composition of *S. eboracensis* using RAPD and ISSR markers (Abbott *et al.*, 2003) showed that eight of 12 markers that are diagnostic of *S. vulgaris* were present in all individuals of *S. eboracensis* examined, along with six of nine markers diagnostic of *S. squalidus*. The high proportion of *S. squalidus* markers in *S. eboracensis* indicates that the new species may contain a large portion of the genome of *S. squalidus*, assuming that such markers are distributed throughout the *S. squalidus* genome rather than being restricted to a small part of it. It would follow that in the formation of *S. eboracensis*, a large part of the genome of *S. vulgaris* may have been replaced by the *S. squalidus* genome. If *S. vulgaris* is an allopolyploid (Ashton & Abbott, 1992b), it is feasible that one of its two genomes has been largely replaced by the *S. squalidus* genome to give rise to *S. eboracensis*. However, if *S. vulgaris* is an autopolyploid (Kadereit, 1984; see Comes *et al.*, 1997), then it is possible that a large part of half of its duplicated genome has been replaced during the origin of the new species. A detailed investigation of the genome structure of *S. eboracensis* and its parents, plus an analysis of chromosome pairing during meiosis, is required to distinguish between various scenarios for the recombinant origin of *S. eboracensis*. Lowe (1996) reported that meiotic cells of one partially fertile  $F_2$  plant of a cross between *S. eboracensis* and *S. vulgaris* exhibited 19 bivalents and two univalents, indicating a lack of homology between only one pair of chromosomes. Consequently, it cannot be ruled out that *S. eboracensis* originated following the introgression of one *S. squalidus* chromosome into *S. vulgaris*, although this seems unlikely given the close morphological resemblance of *S. eboracensis* to *S. cambrensis*.

An attempt to clarify the pathway of origin of *S. eboracensis* has been made by Lowe & Abbott (2000) by means of artificial resynthesis. Fertile tetraploid hybrid offspring of *S. vulgaris* and *S. squalidus* similar in morphology to *S. eboracensis* were formed among  $F_2$  and  $F_3$  progeny of the cross and more commonly among progeny of backcrosses to *S. vulgaris*. The  $F_1$  is normally triploid and highly sterile, and consequently tetraploid segregant and backcross offspring are likely to result from occasional formation of balanced diploid gametes by the hybrid. However, one  $F_1$  produced by Lowe & Abbott (2000) was tetraploid and exhibited relatively high pollen and seed fertility. This was probably formed by fusion of a diploid (unreduced) gamete of *S. squalidus* with a normal reduced gamete of *S. vulgaris*. It is feasible therefore that *S. eboracensis* was produced by either the production of a sterile triploid or fertile tetraploid  $F_1$  between

*S. vulgaris* and *S. squalidus*, followed by segregation or backcrossing of the hybrid to *S. vulgaris*. Lowe & Abbott (2000) argued that a stable form of *S. eboracensis* could have been produced by either of these routes in only a few generations.

## ESTABLISHMENT

Following its origin, a polyploid or homoploid hybrid neospecies will usually occur at low frequency in sympatry with its parents, and may suffer a minority type disadvantage if it reproduces by outcrossing (Husband, 2000; Levin, 2002; Pannell *et al.*, 2004). This is because most offspring will result from crosses with the parents and are likely to be sterile or exhibit low fertility (Levin, 1975; Felber, 1991). This disadvantage will be avoided if prezygotic isolation prevents or reduces significantly the production of such offspring. Theoretical modelling shows that predominant selfing, a clumped distribution (McCarthy, Asmussen & Anderson, 1995) or ecological differentiation (Buerkle *et al.*, 2000) can favour the sympatric establishment of a new hybrid lineage. It has been suggested that selfing may be common in allopolyploids, whereas many hermaphroditic autopolyploid species have mixed mating systems with intermediate or high outcrossing rates (see Galloway, Etterson & Hamrick, 2003). If this pattern is confirmed over a large number of polyploid species, it would indicate that selfing may often be a key factor in the establishment of newly originated allopolyploids, whereas other forms of prezygotic isolation are important in the establishment of new autopolyploids (see Husband & Schemske, 2000).

Both *S. cambrensis* and *S. eboracensis* are self-compatible (Irwin & Abbott, 1992; Ingram & Noltie, 1995) and will exhibit a high level of prezygotic reproductive isolation from each parent if they reproduce by predominant selfing in the wild. Ingram & Noltie (1995) examined the progeny of a non-radiate form of *S. cambrensis*, which was a minority component of a population composed largely of radiate individuals, i.e. individuals producing capitula with ray florets. Of 519 offspring sampled from ten open-pollinated plants, 14 (2.7%) were short-rayed and the product of crosses between non-radiate and radiate plants. This low level of outcrossing is equivalent to that recorded for non-radiate *S. vulgaris* (Marshall & Abbott, 1982, 1984). The outcrossing rate of the usual radiate form of *S. cambrensis* is expected to be higher and possibly within the same range as that recorded for radiate *S. vulgaris*, i.e. 6–35% (Marshall & Abbott, 1982, 1984), which is still low enough to provide effective prezygotic reproductive isolation from both parent taxa. Hybrids produced experimentally between *S. cambrensis* and *S. squalidus* are very infertile and show a high degree of meiotic irregularity, whereas

*S. cambrensis* × *S. vulgaris* hybrids are vigorous and fairly fertile (Ingram & Noltie, 1995). However, neither hybrid has been recorded in the wild, indicating that hybridization between ploidal levels either does not occur or occurs very rarely under these conditions (Ingram & Noltie, 1995).

Hybrids between *S. eboracensis* and *S. squalidus* have been generated (Lowe & Abbott, 2004) and were triploid and highly sterile (0.63% seed set when left to open-pollinate, and 36.6% pollen fertility). On average, two trivalents and 4–8 univalents were produced in meiotic cells of one hybrid examined, demonstrating a high level of meiotic irregularity (Lowe, 1996). The fertility of  $F_2$  offspring increased to 23.9% and 69.5% for seed and pollen fertility, respectively, whereas offspring produced by backcrossing the  $F_1$  to *S. eboracensis* had mean seed and pollen fertilities of 55.4% and 65.5%, respectively. Hybrids between *S. eboracensis* and *S. vulgaris* are more easily made and have pollen fertility and seed set means not significantly different from those of one or other parent (Lowe & Abbott, 2004). Mean seed set of  $F_2$  plants is significantly lower than those of either parent; however, seed set varies greatly among individuals with some producing no viable seed whereas others have seed set values up to 89%. Backcross progeny also exhibit a considerable range of seed set values, with a mean lower than those of the parents, but not significantly different from that of *S. eboracensis*.

From these results, it is evident that if matings between *S. eboracensis* and *S. squalidus* were frequent in populations in which *S. eboracensis* was in the minority, the new species would suffer an acute minority type disadvantage because most of its offspring would be hybrid and highly sterile. By contrast, frequent matings between *S. eboracensis* and *S. vulgaris* would lead to rapid erosion of the identity of the new taxon, as hybrid and backcross offspring exhibit relatively high fertility.

No hybrids between *S. eboracensis* and *S. squalidus* have been recorded in the wild despite thorough searching over several years. Moreover, the level of hybridization between the two taxa was only 0.1% in an experiment aimed to maximize natural hybridization by surrounding individual plants of *S. eboracensis* with several plants of *S. squalidus* at times when pollinators were plentiful (Lowe & Abbott, 2004). It is concluded that these two taxa seldom hybridize and therefore *S. eboracensis* would not suffer greatly from a minority type disadvantage due to interspecific crossing in mixed populations with *S. squalidus*.

Hybrids between *S. eboracensis* and *S. vulgaris* also form rarely (Lowe & Abbott, 2004). At one site in York where both taxa occurred in relatively high numbers,

two mature hybrids were found in one year and none the following year. Tests of *S. eboracensis* progeny showed that rates of intertaxon crossing varied between 0 and 1.46% in one year, depending on sampling date, and was zero the following year. No hybrids were detected among progeny of *S. vulgaris* produced in either year. The amount of hybridization between the two species will depend on their spatial arrangement in a population. Thus, when individuals of *S. eboracensis* were surrounded by plants of non-radiate *S. vulgaris* in a common garden experiment at St Andrews, the frequency of hybrids among offspring of *S. eboracensis* reached 18.3%. By contrast, the frequency of hybrids was only 1.4% among progeny of non-radiate *S. vulgaris* plants surrounded by plants of *S. eboracensis* (Lowe & Abbott, 2004).

Hybridization is rare between *S. eboracensis* and *S. vulgaris* because both species reproduce mainly by selfing. A high selfing rate has been demonstrated for *S. vulgaris* (Marshall & Abbott, 1982, 1984) and is also presumed for *S. eboracensis* given that the capitula of this species are not much different in size from those of radiate *S. vulgaris*. Additional factors that will reduce hybridization are differences in flowering time and non-random spatial distribution within mixed populations. We found that in York, *S. vulgaris* flowered mainly from April to June, whereas *S. eboracensis* flowered from May to July (Lowe & Abbott, 2004). In the same population, an analysis of the spatial distribution of adult plants revealed significant clumping of conspecifics. Given the expected greater attractiveness of radiate *S. eboracensis* relative to non-radiate *S. vulgaris* (see Abbott & Irwin, 1988), pollinator visitation is likely to be more common within and between clumps of *S. eboracensis* than between clumps of the two species.

The very low rates of hybridization recorded between *S. eboracensis* and *S. vulgaris* in the wild shows that a strong prezygotic reproductive barrier exists between them and consequently the establishment of *S. eboracensis* will not be materially affected by the possibility of interbreeding with *S. vulgaris* and subsequent introgression.

## EVOLUTION

Following the origin and establishment of a new polyploid species, it is of interest to determine how quickly alterations to genome and gene expression occur, and the potential that exists for rapid adaptation to changed environmental conditions. Alterations to genome structure and size in allopolyploids can result from intragenomic translocations and inversions, intergenomic recombination following homoeologous chromosome pairing at meiosis, and the activation of transposable elements and retroele-

ments (see Levin, 2002; and Chen *et al.*, 2004; Kovarik *et al.*, 2004; Lim *et al.*, 2004; Lukens *et al.*, 2004; Levy & Feldman, 2004 – all this issue). Although both wild and artificially synthesized material of *S. cambrensis* show high levels of bivalent formation at meiosis (Ingram & Noltie, 1989), the results of an examination of the genetic control of capitulum type suggest that homoeologous chromosome pairing during quadrivalent formation is likely to be an important source of variation (Ingram & Noltie, 1984) and may have been responsible for the origin of a rare non-radiate form of *S. cambrensis* in North Wales and Edinburgh. It is also known that whereas Welsh *S. cambrensis* possesses an additive nuclear rDNA restriction profile that combines the profiles distinguishing its parents, most Edinburgh material has a profile identical to that of *S. vulgaris* (Harris & Ingram, 1992; Lowe & Abbott, 1996). This may suggest that in Edinburgh material rDNA repeats have undergone rapid concerted evolution (Dover, 1982), resulting in interlocus homogenization with a bias to the maternal parent and a loss of *S. squalidus* rDNA. There is currently little evidence that *S. cambrensis* has undergone evolutionary change in genome size, as its genome size (2C DNA level = 5.15 pg) approximates that of the sum of the two parents (*S. squalidus* = 1.80 pg, *S. vulgaris* = 3.15 pg, Bennett & Leitch, 2003).

In summary, there is some evidence to indicate that *S. cambrensis* has undergone rapid evolution in genome composition since its origin. Research is currently underway to compare the structure of the genome of wild material of *S. cambrensis* with those of its parents and newly synthesized material of *S. cambrensis* to establish the amount and speed of genomic change since the species originated. This entails the construction and comparison of genetic linkage maps for each of the species involved. Further research is ongoing to examine possible alterations to gene expression in wild and synthetic material of *S. cambrensis* using microarray analysis. Similar work conducted on *S. eboracensis* would be desirable.

### EXTINCTION

Although many allopolyploid species are known to have originated more than once and sometimes on multiple occasions (Soltis & Soltis, 1993; Doyle *et al.*, 2004 – this issue; Soltis *et al.*, 2004), there is little information concerning the relative survival and extinction of different lineages formed in this way. Novak, Soltis & Soltis (1991) have reported the rapid turnover of populations of the two new *Tragopogon* allopolyploids, *T. mirus* and *T. miscellus*, in north-west North America and discussed how this might

lead to the elimination of some lineages. However, the only published information on lineage extinctions as far as we know comes from monitoring Welsh and Edinburgh populations of *S. cambrensis* known to be products of independent origins. Whereas in Wales *S. cambrensis* has expanded its range in the area around Wrexham since it was first recorded at Cefn-y-bedd in 1948 (Ingram & Noltie, 1995; Fig. 1), and has maintained a population disjunctly at Mochdre (R. J. Abbott, pers. observ.), the Edinburgh lineage is now extinct (Abbott & Forbes, 2002). Despite extensive searches, the last record of the species in Edinburgh was made in 1993. It is concluded that the Edinburgh lineage survived at least 19 years since it was first recorded in the wild in 1974. The extinction of *S. cambrensis* in Edinburgh would appear to stem mainly from an inability to expand rapidly the number and size of its populations due to a reduction in number of disturbed sites available for colonization in Edinburgh during the late 1980s and early 1990s (Abbott & Forbes, 2002). The maximum number of individuals recorded for the lineage in any one year was 102 in 1982 when the species was discovered in Edinburgh and occurred on six different sites. In 1993, only three individuals of the species were recorded and were restricted to a single site. By 1993, four of the original sites had been built on and were no longer available for colonization.

New species are likely to be most vulnerable to extinction immediately after their origin when they are represented by very few individuals, which can be exterminated relatively easily by chance (see Novak *et al.*, 1991, for discussion). The new species, *S. eboracensis*, is currently highly endangered because of this, and redevelopment or intensive weeding of its existing sites could drive it to extinction very quickly.

### CONCLUSIONS

The discovery of *S. cambrensis* and *S. eboracensis* soon after their recent origin in the British Isles provides an unparalleled opportunity for examining two different but related forms of hybrid speciation. Both of these species are products of hybridization between a native tetraploid species, *S. vulgaris*, and an introduced diploid species, *S. squalidus*. *S. cambrensis* has originated via allopolyploidy on two separate occasions, first in North Wales and later in Edinburgh, whereas *S. eboracensis* originated via recombinant polyploid speciation and is restricted to York, England. A third taxon, which is a product of hybridization between the same two parent species, is the radiate variant of *S. vulgaris*, var. *hibernicus*. This is a stable tetraploid ( $2n = 40$ ) introgressant that is believed to contain only a very small portion of genome intro-



gressed from *S. squalidus* (Abbott, Ashton & Forbes, 1992; Abbott *et al.*, 2003), and is not discussed in any detail in this paper. The two new species reproduce by predominant selfing, so will not be greatly affected by either the minority type disadvantage or gene swamping caused by interspecific gene flow during establishment in sympatry with a parent. However, their successful establishment will be affected by chance demographic factors during the period that numbers of individuals within populations and numbers of populations at different sites remain low (Novak *et al.*, 1991; Levin, 2000). Thus, it is essential for a new species to expand rapidly in number and range to improve its chance of long-term survival. Further analysis of the ecology and genomics of the two new species should improve greatly our understanding of their evolution and therefore the processes of polyploid speciation in plants.

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